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# Morphological Variability of *Mertensia pterocarpa* (Turcz.) Tatew. & Ohwi (Boraginaceae) in Hokkaido and the Southern Kurils

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Mertensia pterocarpa var. yezoensis of Hokkaido has been distinguished from M. pterocarpa var. pterocarpa of the southern Kurils mainly by the hairiness and shape of the calyx lobes. The hairiness on the outside of the calyx lobes exhibits a geocline from glabrous or sparsely strigose in the southern Kurils on the one end, through eastern Hokkaido, the Taisetsu Range and the Yubari Range, to densely strigose on Mt. Tottabetsu of the Hidaka Range on the other. The shape of the calyx lobes shows no such geocline. The calyx sometimes shows characteristic features for each mountain; e.g., narrow calyx lobes on Mt. Yubari, but otherwise can be very variable even on a single mountain; e.g., lobes lanceolate to deltoid on Mt. Tottabetsu. Principal component analysis using six morphological characters indicated that the range of variation in plants of the Hidaka-Yubari Ranges (typical var. yezoensis) is a distinct from that in plants of the southern Kurils (typical var. pterocarpa), but the range of variation in plants of the Taisetsu Range is broad and encompasses ranges of variation of both the Hidaka-Yubari and southern Kuril populations. The plants of M. pterocarpa from the southern Kurils, the Taisetsu Range, and the Hidaka-Yubari Ranges are morphologically similar. Plants from Mt. Nagayama, half of the plants from Mt. Kami-Furano and some plants from Mt. Byobu of the Taisetsu Range are especially similar to those of the southern Kurils and should be treated as var. pterocarpa. Not only var. yezoensis but also var. pterocarpa, together with plants intermediate between them, grow on Hokkaido.

Key words: calyx lobes, Hidaka, Hokkaido, Mertensia pterocarpa, Mertensia pterocarpa var. yezoensis, southern Kurils, Taisetsu, Yubari

Many infraspecific taxa of plant species in Japan and adjacent regions have been described, but their distinction from typical forms has been based mostly on typological studies. For most, no sufficient quantitative analyses of morphological features have been carried out to substantiate the recognition of the infraspecific taxa. Careful analysis of representatives of the species throughout its full range is necessary to determine.

Mertensia, with about 50 species (Boraginaceae) is widely distributed mainly in the north temperate zone (Shaw 1973). Mertensia pterocarpa (Turcz.) Tatewaki & Ohwi, a perennial alpine herb, occurs on Hokkaido and in the southern part of the Kurils.

Based on the plants from the Yubari Range, Hokkaido, Ohwi (1933b) distinguished *M. pterocarpa* var. *yezoensis* Tatewaki & Ohwi from var. *pterocarpa* of the southern Kurils by its narrower ovate leaves (vs. mostly broadly ovate leaves), lanceolate, acute calyx lobes (vs. mostly oblong-linear), and sparsely strigose outer surface of the calyx lobes (vs. glabrous). Although variation in those morphological characters in Hokkaido has never been examined, the recent floristic works in Japan (Murata 1981, Shimizu 1982, Ohwi & Kitagawa 1983, Yamazaki 1993) follow Tatewaki and Ohwi (Ohwi 1933a, 1933b) in recognizing only *M. pterocarpa* var. *yezoensis* on Hokkaido and var. *pterocarpa* in the southern Kurils. We dis-

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covered that some plants from Hokkaido are indistinguishable from those of the southern Kurils using those characters, and a broad range of inter- and intra-mountain range variation was discovered in herbarium specimens from Hokkaido. In this study, we examined specimens of *M. pterocarpa* from Hokkaido and the southern Kurils thoroughly to determine the quantitative morphological variation in this species. Such analyses may clarify infraspecific taxonomic problems and shed light on the processes of intraspecific differentiation in *M. pterocarpa*.

#### Materials and Methods

## Samples

Our morphological studies are based on specimens deposited in the following herbaria; KYO, Herbarium,

Kyoto University; SAPS, Herbarium, The Hokkaido University Museum, Sapporo; TNS, National Science Museum, Tokyo; WTU, Herbarium, Department of Botany, University of Washington, Seattle. In total, we examined 104 plants from Hokkaido and 49 plants from the southern Kurils (Table 1).

In Hokkaido, *Mertensia pterocarpa* occurs usually in mountainous areas above 1000 m in altitude. All the specimens from Hokkaido were collected in the Central Plateau (we use "Taisetsu Range" in a broad sense here), the Hidaka Range, the Yubari Range, Mt. Shari and Mt. Shokanbetsu. The specimens examined cover all these areas (Fig. 1). Since the specimen from Mt. Shokanbetsu was made from a plant in cultivation, we treat the data from it only as reference data. From the Kurils, we examined specimens from Shikotan, Kunashir and Iturup islands.

TABLE. 1. Specimens of *Mertensia pterocarpa* used for quantitative morphological analysis.

Localities and voucher specimens	No. of plants examined
HOKKAIDO	
1. Hidaka Range, Hokkaido	
Mt. Tottabetsu, Hidaka-side, Sep. 8, 1933, Y. Hoshino s.n. (SAPS)	2
Mt. Tottabetsu 1600-1700m, Aug. 1935, collector unknown (SAPS)	6
2. Yubari Range, Hokkaido	
Summit of Mt. Yubari, Jun. 1894, T. Ishikawa s.n. (SAPS)	2
Mt. Yubari, Sep. 9, 1987, <i>H. Takahashi et al. 8060</i> (SAPS)	1
Mt. Yubari, Jul. 29, 1987, <i>H. Takahashi et al. 7532</i> (SAPS)	3
Mt. Yubari, Jul. 9, 1989, <i>Y. Aida 415</i> (KYO)	2
Mt. Ko-Yubari, Aug. 4, 1921, <i>H. Takeda &amp; M. Tatewaki s.n</i> . (SAPS)	1
Mt. Ashibetsu, Jul. 28-31, 1915, H. Koidzumi s.n. (SAPS)	4
Mt. Ashibetsu, 1915, <i>H. Koidzumi s.n.</i> (KYO)	2
Mt. Ashibetsu, Jul. 30, 1915 H. Koidzumi 74009 (TNS)	4
Mt. Ashibetsu, Aug. 5, 1913, <i>H. Yanagisawa s.n.</i> (SAPS)	1
Mt. Ashiupetnupuri, Aug.3-5, 1913, S. Nishida & H. Yanagisawa s.n. (SAPS)	8
Gama-iwa, Jul. 22-26, 1928, <i>H. Koidzumi 17061</i> (TNS)	1
3. Mt. Shokanbetsu, Hokkaido	
Mt. Shokanbetsu (cult. in Yoichi), Jun., 1936, I. Yamamoto s.n. (SAPS)	4
4. Taisetsu Range, Hokkaido	
Mt. Furano, Sep. 6, 1947, <i>M. Tatewaki 36205</i> (SAPS)	11
Mt. Kami-Furano, Aug. 9, 1915, <i>H. Koidzumi 74218</i> (TNS)	3
Mt. Kami-Furano, Jul. 14, 1917, <i>H. Koidzumi 77084</i> (TNS)	4
Mt. Kami-Furano, Jul. 14, 1917, <i>H. Koidzumi 77086</i> (TNS)	3
Mt. Kami-Furano, Jul. 19, 1917, <i>H. Koidzumi 77697</i> (TNS)	3
Mt. Tokachi, <i>S. Sugawara 18850</i> (SAPS)	1
Mt. Oputateshike, Aug. 10, 1956, S. Watanabe 3737 (KYO)	2
Mt. Tomuraushi, Jul. 29, 1919, <i>H. Koidzumi 80631</i> (TNS)	2
Mt. Tomuraushi, 1955, <i>G. Murata &amp; Y. Momotani 236</i> (KYO)	4
Mt. Chubetsu-hontake, Aug. 19, 1926, H. Koidzumi 54161 (TNS)	1
Mt. Chubetsu-hontake, Aug. 19, 1927, H. Koidzumi 15070 (TNS)	1

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TABLE. 1. continued

ocalities and voucher specimens	No. of plant
	examined
Sannonuma, Aug.19, 1958, R. Nakajo s.n. (SAPS)	2
South of Mt. Nagayama, Aug. 18-21, 1926. H. Koidzumi 53301 (TNS)	6
Mt. Nagayama, Aug. 19, 1926. <i>H. Koidzumi 12688</i> (TNS)	5 1
Mt. Nipesotsu, Aug.1, 1932, <i>Y. Tokunaga s.n.</i> (SAPS)	
Mt. Ura-Nipesotsu, Aug. 26, 1927, <i>H. Koidzumi, 54288</i> (TNS)	2
Mt. Ishikari, Aug. 2, 1932, <i>Y. Tokunaga s.n.</i> (SAPS)	
Mt. Niseikaushupe, Aug. 24-27, 1926, H. Koidzumi 53557 (TNS)	4 1
Mt. Niseikaushupe, Aug. 26, 1926, <i>H. Koidzumi 13216</i> (TNS)	
Mt. Niseikaushupe, Aug. 9, 1947, M. Tatewaki & J. Samejima 35392 (SAPS)	2
Mt. Dai-Byobu, Aug. 24-27, 1926, <i>H. Koidzumi 53556</i> (TNS)	3
5. Mt. Shari, Hokkaido	
Mt. Shari, Aug. 19, 1984, <i>K. Takita 2132</i> (KYO)	1
SOUTHERN KURILS	
5. Shikotan Isl., Kurils	
Matakotan, Jul. 19, 1931, <i>J. Ohwi 25</i> (KYO)	2
Mt. Shikotan, Jul. 17, 1909, H. Takeda s.n. (SAPS)	2
Mt. Shikotan, Jun. 29, 1934, M. Tatewaki 20796 (SAPS)	1
Shakotan, Jul. 8, 1930, S. Ohno, s.n. (SAPS)	1
Shakotan, 1930, S. Ohno s.n. (KYO)	2
Shakotan, Aug. 7, 1910, G. Tanaka & Ken. Miyabe s.n. (SAPS)	1
Near Shakotan, Aug . 23, 1927, M. Tatewaki 9507 (SAPS)	1
Shakotanzaki, Jul. 27, 1931, <i>J. Ohwi 266</i> (SAPS)	3
Shakotanzaki, Jul. 27, 1931, <i>J. Ohwi 266b</i> (KYO)	4
Shakotanzaki, Jul. 29, 1931, <i>J. Ohwi 344</i> (KYO)	2 1
Shakotanzaki, Jun. 29, 1934, <i>M. Tatewaki 20820</i> (SAPS)	4
Umanose, Aug. 30, 1931, <i>J. Ohwi 1073</i> (KYO)	4
7. Kunashir Isl., Kurils	2
Mt. Rurui, Jul. 22, 1935, <i>K. Shirahama &amp; Y. Takahashi s.n.</i> (SAPS)	2
3. Iturup Isl., Kurils	4
Near Moikeshi Bay (1000m), Aug. 18, 1890, <i>T. Ishikawa s.n.</i> (SAPS)	1
Naibo-Toro, Aug. 1890, <i>M. Kambe s.n.</i> (SAPS)	2
Mt. Atosa, Aug. 14, 1939, <i>B. Yoshimura s.n.</i> (SAPS)	2
Oito, Aug. 26, 1895, <i>Tanaka s.n.</i> (SAPS)	2
Minami-Chirippu, Jul. 24, 1938, B. Yoshimura & H. Yokoyama s.n. (SAPS)	ı
Sentyabrisky, Jul. 29, 1998, N. Minakawa SLJ-000119 (WTU)	]
Toshiruri, Sep. 20, collector unknown (SAPS)	1
Porosu, Jul. 7, 1898, <i>T. Kawakami 33</i> (SAPS)	1
Porosu, Aug. 8, 1898, <i>T. Kawakami s.n.</i> (SAPS)	1
Porosu, Aug. 18, 1930, <i>H. Koidzumi 25247</i> (TNS)	2
Porosu-Toro, Jul. 1893, <i>S. Yokoyama s.n.</i> (SAPS)	1
Porosu-Sokiya, Jul. 30, 1938, B. Yoshimura & H. Yokoyama s.n. (SAPS)	3
Shibetoro-Sokiya, Jul. 20, 1910, <i>G. Tanaka &amp; Ken. Miyabe s.n.</i> (SAPS)	2
Mt. Rakkibetsu Aug. 19, 1930, H. Koidzumi 25785 (TNS)	2
Moyoroato, Aug. 16, 1930, <i>H. Koidzumi 25460</i> (TNS)	1

1) Holotype of *M. pterocarpa* var. *yezoensis* (Ohwi 1933)

We also examined the holotype specimen of *M. pte-rocarpa* var. *yezoensis* (Ohwi 1933b) and specimens cited as *M. pterocarpa* var. *pterocarpa* by Ohwi (1933a).

# Characters examined

The number of hairs on the outside of the calyx lobes (excluding marginal ones) was counted under a stereoscopic microscope. The most densely strigose calyx lobe on each plant was selected for evaluation.

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The largest calyx lobe on each plant was selected for the length and width measurement. The length from the base to the widest part of the calyx lobe was also measured, and its proportion to the calyx lobe length was calculated (in the following text, we use 'percentage to widest part'). The calyx lobe shape was determined by the width/length ratio and the percentage to widest part.

The largest leaf on each plant was selected for the measurement of the leaf width/length. Plant height was also measured.

In total, six morphological characters (number of hairs on outside of calyx lobe, calyx lobe length and width, percentage to widest part of calyx lobe, leaf width/length ratio and plant height) were used for a principal component analysis (PCA).

### Results

Hairs on calyx lobes

Geographical variation in the number of hairs on the outside of the calyx lobes is shown in Fig 1. The plants from Shikotan, Kunashir and Iturup had 0-2 hairs on the calyx lobes. On Hokkaido, all the plants from Mt. Shari, Mts. Ishikari and Nipesotsu (the eastern part of the Taisetsu Range) and some plants from Mts. Byobu and Niseikaushupe (the northern part of the Taisetsu Range) and Mts. Nagayama, Tomuraushi and Kami-Furano (the central to southern parts of the Taisetsu Range) also had 0-2 hairs. Plants with denser hairs were from the central to southern parts of the Taisetsu Range, especially on Mt. Tomuraushi (to 20 hairs) and Mt. Oputateshike (10-14 hairs).

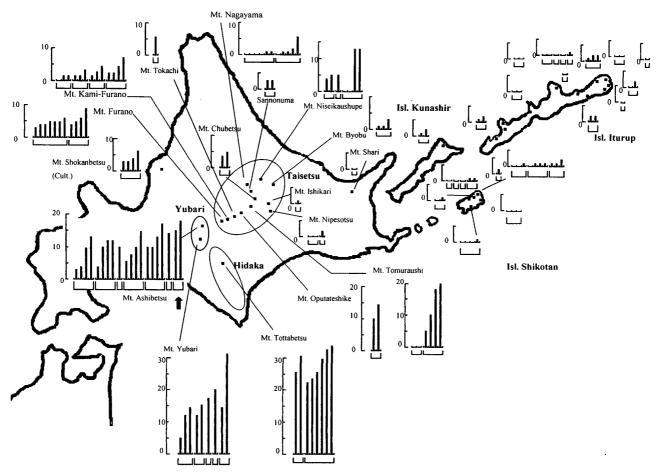


Fig. 1. Number of hairs on outer surface of calyx lobes. Vertical bar indicates value of each plant. For each mountain or locality, bar bound by line below graph indicates the plants from the same collection. Arrow indicates holotype specimen of *Mertensia pterocarpa* var. *yezoensis*.

Plants from Mt. Tottabetsu of the Hidaka Range have the densest hairs (22-33) in Hokkaido. Plants from the Yubari Range (Mt. Yubari and Mt. Ashibetsu) have somewhat dense hairs (3-32, mainly 4-18). Thus the hairiness of the outside of the calyx lobes shows a geocline; from 0-2 in the southern Kurils, through 0-20 in eastern Hokkaido and the Taisetsu Range, 3-32 in the Yubari Range to 22-33 in the Hidaka Range. The holotype of var. *yezoensis* collected on Mt. Ashibetsu of the Yubari Range (Ohwi 1933b) has 15-18 hairs.

# Shape and size of calyx lobes

Width/length ratios of the calyx lobes on plants from Hokkaido generally are lower than those from plants of the southern Kurils; 90% of the Hokkaido speci-

mens were within a variation range of 0.15 - 0.25, showing great variability in plants of the Taisetsu Range (Fig. 2). More than 90% specimens of the southern Kurils were within a variation range of 0.18 - 0.26. The calyx lobes of the Hokkaido plants generally have a broad base and narrowed tip, and more than 90% of the plants from Hokkaido are situated within a variation range of 10-45% in percentage to widest part (deltoid to lanceolate), whereas more than 90% of the plants of the southern Kurils have more elliptic calyx lobes, with a range of 30-50% (Fig. 2). No clear discontinuity was detected in this character between Hokkaido and the southern Kurils because all the plants of Mt. Nagayama (NG) and some plants from Mts. Kami-Furano (KF), Niseikaushupe (NS) and Byobu (BB) of the Taisetsu

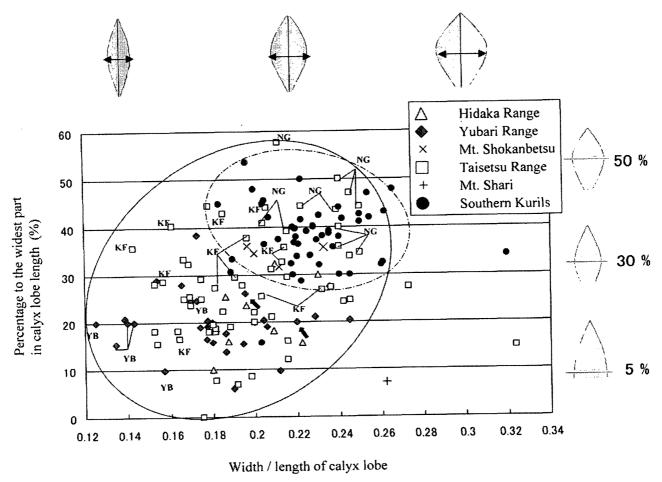


Fig. 2. Width/length ratio and percentage to widest part of calyx lobes. Arrow indicates holotype specimen of *Mertensia pterocarpa* var. *yezoensis*. Localities: BB, Mt. Byobu; KF, Mt. Kami-Furano; NG, Mt. Nagayama; NP, Mt. Nipesotsu; NS, Mt. Niseikaushupe; YB, Mt. Yubari. Solid line demarcates most specimens from Hokkaido; broken line demarcates most specimens from southern Kurils.

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Range, Hokkaido, are within the range of variation of plants from the southern Kurils (Fig. 2).

The calyx lobe shape shows a broad range of inter- and intra-mountain range variation on Hokkaido. In the Taisetsu Range, plants from Mt. Nagayama (NG) and Mt. Kami-Furano (KF) tend to have more lanceolate calyx lobes with high values of the percentage to widest part (mainly 25-50%; Fig. 2), similar to the calyx lobe shape of plants from the southern Kurils. Plants from other mountains in the Taisetsu Range tend to have more deltoid calyx lobes (mainly 5-35%). The calyx lobes of plants from the Hidaka Range (Mt. Tottabetsu) also show variation from deltoid to lanceolate (10-30%). In the Yubari Range, the calyx lobes of Mt. Yubari (YB in Fig. 2) are characteristically narrower (less than 0.18 in width/length ratio) than in plants from Mt. Ashibetsu (gray diamonds without letters).

Although the calyx lobes of plants from Hokkaido tend to be narrower (0.7-1.4 mm) than those of plants from the southern Kurils (0.9-1.7 mm), the values overlap broadly, but nine plants from Mt. Yubari showed constantly narrower calyx lobes (0.7-1.0 mm).

The calyx lobes of the holotype specimen of var. *yezoensis* from Mt. Ashibetsu (indicated by arrows in Fig. 2) in the Yubari Range are nearly average in size and shape among Hokkaido plants (Fig.2).

#### Vegetative characters

Plants are usually shorter on Hokkaido (7-36 cm) than in the southern Kurils (16-58 cm). Leaf width correlates well with calyx lobe width; i.e., narrower (1.4-4 cm) on Hokkaido than on the southern Kurils (1.2-5.7 cm). Similarly, leaf width/length ratio is 0.37-0.89 in Hokkaido and 0.41-1.0 in the southern Kurils, reflecting the broader leaves on plants from the southern Kurils. These values, however, as in calyx lobe characters, overlap broadly between the two regions.

#### Principal component analysis (PCA)

PCA shows that plants from the southern Kurils are not clearly separated from those of Hokkaido (Fig. 3). The percentage to widest part in the calyx lobes (+0.5521 in factor loading), number of hairs on the outside of the calyx lobes (-0.5264) and leaf width/length ratio (+0.4698) mainly contribute to the first component (Table 2). Among Hokkaido plants, all the plants from Mt. Nagayama (NG), almost half of the plants from Mt. Kami-Furano (KF) and some plants from Mt. Byobu (BB) and Mt. Nipesotsu (NP) in the Taisetsu Range are included within the range of plants from the southern Kurils (Fig. 3). The second component, based on calyx lobe length and width, provides little information on differences between plants from Hokkaido and the southern Kurils. The first two components (Fig. 3) explain 57.5% of the total variation. Plant height (+0.8896) contributes

Table. 2. Factor loading, eigenvalue, contribution, and accumulated contribution for principal components.

	Components		
Characters	$\overline{Z_1}$	Z <sub>2</sub>	
Number of hairs on outside of calyx lobes	-0.5264	-0.0538	
Length of calyx lobes	-0.0251	0.7127	
Width of calyx lobes	0.3962	0.5304	
% of length from base to widest part of calyx lobes	0.5521	-0.0350	
Leaf width/length ratio	0.4698	-0.2742	
Height of the plant	0.1996	-0.3626	
Eigenvalue	2.10	1.35	
Contribution (%)	34.92	22.58	
Accumulated contribution (%)	34.92	57.50	

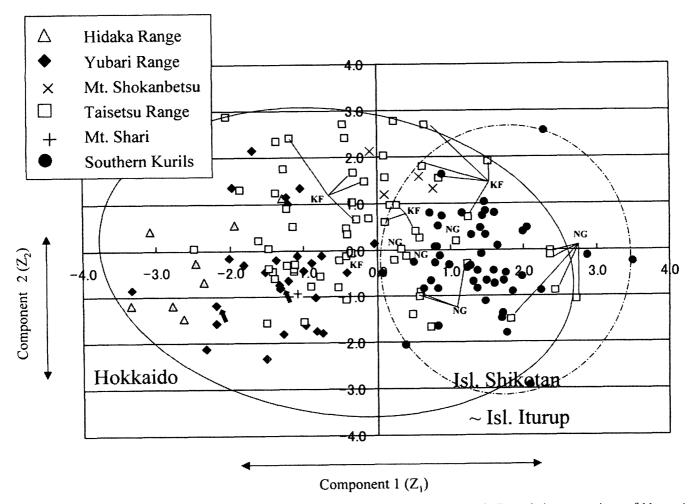


Fig. 3. Principal component analysis using six morphological characters (see Table 2). Arrow indicates holotype specimen of *Mertensia pterocarpa* var. *yezoensis*. Localities: BB, Mt. Byobu; KF, Mt. Kami-Furano; NG, Mt. Nagayama; NP, Mt. Nipesotsu; NS, Mt. Niseikaushupe. Solid line demarcates most specimens from Hokkaido; broken line demarcates most specimens from southern Kurils

significantly to the third component. As this character show wide variation even within the same collection, the third component is not useful for clarifying geographical differences.

Although some plants of Mt. Shokanbetsu are within the range of variation of plants from the southern Kurils (Fig. 3), we have to note that those samples were made from cultivated plants. Considering the uncertainty of the natural distribution on Mt. Shokanbetsu (see discussion), we will not discuss those plants further.

In contrast with plants from the Taisetsu Range, plants of the Hidaka-Yubari Ranges do not overlap with plants of the southern Kurils (Fig. 3). The range of variation of plants from the Hidaka-Yubari Ranges

overlaps widely with plants of the Taisetsu Range.

# **Discussion**

#### Distribution pattern

Mertensia pterocarpa in the Taisetsu Range, the Hidaka-Yubari Ranges and the Mashike Range (Mt. Shokanbetsu) has been recorded by several authors (Kawano 1971, Okuyama 1983, Ito & Hinoma 1987). The reports by Kawano (1971) and Ito & Hinoma (1987) from Mt. Shokanbetsu may be based on a herbarium specimen taken from the cultivated plants listed here (Table 1). Toyokuni's (1951, 1953) floristic works of the area, did not record this species. Okuyama (1983) provided a photograph of plants

from Mt. Shokanbetsu, but his distribution map did not include a dot on Mt. Shokanbetsu. More field studies are necessary to confirm the presence of this species on Mt. Shokanbetsu.

Although the occurrence of *Mertensia ptero-carpa* on Mt. Shari in eastern Hokkaido has not been reported (Toyokuni 1969, Kawano 1971, Okuyama 1983, Ito & Hinoma 1987), there is a collection by Faurie from Mt. Shari in 1890. Recently the plants were collected again by Takita (Table 1, Takita 1987).

The distribution of *Mertensia pterocarpa* is sparse in the eastern Hokkaido - Kunashir region (see Fig. 1). It has not been recorded from the Shiretoko Peninsula in eastern Hokkaido and is rare on Kunashir in the southern Kurils. The present slightly discontinuous distribution pattern makes intraspecific genetic differentiation between Hokkaido and the southern Kurils seem probable.

# Intraspecific morphological differentiation

Morphological variation in *Mertensia pterocarpa* in Hokkaido has not been considered or analyzed previously. We found that the morphological characters of plants from Hokkaido are not uniform, but showing geographic variation.

The calyx lobes of plants of *Mertensia ptero-carpa* from Mt. Yubari and Mt. Tottabetsu, both in the Hidaka-Yubari Ranges, are very narrow and densely hairy, respectively. Plants from Mt. Yubari, Mt. Tottabetsu and Mt. Ashibetsu, in the Hidaka-Yubari Ranges are distinguished from plants of the southern Kurils (Fig. 3) and might be considered to be typical var. *yezoensis*. We have to note, however, that almost half of the plants of the Hidaka-Yubari Ranges cannot be distinguished from plants from the Taisetsu Range because of intermediate plants.

The Hidaka-Yubari Ranges are generally characterized by a lack of moisture, and the prevailing dry alpine flora of this range is due to the steep relief of the mountains. The Taisetsu Range is a high plateau composed of many volcanoes, characterized by rich habitats ranging from wet to dry (Watanabe 1971).

Mertensia pterocarpa grows in fewer localities (three mountains) in the Hidaka-Yubari Ranges than in the Taisetsu Range (twelve mountains). Furthermore, the Hidaka-Yubari Ranges are situated at the southwestern edge of the geographical distribution of this species. Thus, the presence of the typical plants of var. yezoensis in the Hidaka-Yubari ranges may be explained in part by the isolated habitats and the geographical position of the Hidaka-Yubari Ranges on Hokkaido.

Since all of the plants from Mt. Nagayama, nearly half of the plants from Mt. Kami-Furano and some plants from Mt. Byobu in the Taisetsu Range are indistinguishable from plants from the southern Kurils (Figs. 1, 2 and 3), they should be assigned to var. *pterocarpa*. As a result, *Mertensia pterocarpa* var. *pterocarpa* is not restricted to the southern Kurils, but also occurs in the Taisetsu Range on Hokkaido. It is difficult to determine some plants from several mountains (Mts. Kami-Furano, Byobu, Nipesotsu and Niseikaushupe) in the Taisetsu Range as either variety. Both varieties *yezoensis* and *pterocarpa*, together with the intermediate plants, grow in Hokkaido.

Our observations show that *Mertensia ptero-carpa* cannot be recognized solely on the basis of geography, but must be evaluated using morphological criteria. The intraspecific genetic differentiation between Hokkaido and the southern Kurils, which had been expected because of the discontinuous distribution between the two regions, was not confirmed by morphological analysis.

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